

Mons^e Cl. Bernard 6
with the Author's friendly regards

S H E L L.

BY

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(From the *Cyclopædia of Anatomy and Physiology.*)

SHELL.—This term is commonly employed to designate the hard envelopes in which the bodies and members of many animals belonging to the Radiated, Molluscous, and Articulated sub-kingdoms are enclosed. Generally speaking, it is applied to those only into whose composition mineral matter enters: thus, we speak of the shell of a Crustacean, whilst we do not give that appellation to the dermo-skeleton of an Insect or Myriapod. Still this rule is not strictly observed; for there are many Crustacea and Mollusca which are commonly spoken of as possessing shells although these bodies are entirely destitute

of calcareous matter, being as horny in their texture as the envelope of a beetle or a centipede. Among radiated animals, the class of ECHINODERMATA is the only one in which shells are met with; and these are by no means universally present throughout the group. In the *molluscous* series, we meet with shells in every class save the TUNICATA; all the animals of the class CONCHIFERA, whether *lamelli-brachiate* or *pallio-brachiate*, being furnished with them; a considerable proportion of GASTEROPODA (all of them, it would seem, in the embryonic state) possessing them; whilst they are occasionally found in the deli-

cate little PTEROPODA, and in the comparatively gigantic CEPHALOPODA. In this last class, however, the shells are not unfrequently *internal*; an approach to this arrangement being seen in certain Gasteropoda and Pteropoda, in which the shells are covered-in by folds of the mantle, whilst really external to the body. In the *articulated* series, the presence of a shelly covering, according to the usual acceptation of the term, is more restricted. It is possessed by a few ANNELIDA (e. g. *Serpula*, *Spirorbis*, &c.), whose shelly tubes so much resemble those of certain Mollusks as to be readily confounded with them. It is usually found, too, in the CIRRHOPODA, (a class whose articulated character is now quite settled); and it is generally present in the CRUSTACEA, although it is only in the larger and more highly developed forms of this class, that the shell is consolidated by mineral deposit, and really deserves the appellation.

The external configuration of the principal varieties of shelly covering having been sufficiently described under the several heads above referred to, it is not requisite here to revert to that subject; our present purpose being to give an account of the *intimate structure* of shell, on which an entirely new light has been thrown by microscopic enquiries. The prevalent doctrine respecting the nature of shell, as expressed even by the most recent conchological writers, has been that it is not only *extravascular*, but completely *inorganic*, being composed of an *exudation* of calcareous particles, cemented together by animal glue. It may now, however, be stated as an ascertained fact, that shell always possesses a more or less distinct organic structure*; this being in some instances of the character of that of the *epidermis* of higher animals, but in others having more resemblance to that of the *dermis*, or true skin. The nature of the organic structure is so entirely different in the Mollusca, Echinodermata, and Crustacea respectively, that a separate description is required for each; indeed, even in the subordinate divisions of these groups very characteristic diversities are frequently observable; so that, as in the case of teeth, it is often possible to determine the family, sometimes the genus,

* The idea that such would prove to be the case was expressed by the author of this article in the 2d edition of his "Principles of General and Comparative Physiology" (published in 1841), as follows:—"The dense calcareous shells of the Mollusca, and the thinner jointed envelopes of the Crustacea, have been commonly regarded as mere exudations of stony matter, mixed with an animal glue secreted from the membrane which answers to the true skin. The hard axes and sheaths of the Polypifera, however, have been also regarded in the same light; and yet, as will hereafter appear, these are unquestionably formed by the consolidation of what was once living tissue. From the analogy which the shells of Mollusca and Crustacea bear to the epidermic appendages of higher animals, there would seem reason to believe that the former, like the latter, have their origin in cells, and that these are afterwards hardened by the deposition of earthy matter in their interior." P. 33.

and occasionally even the species, from the inspection of a minute fragment of a shell, as well fossil as recent; whilst the degree of correspondence or difference in the intimate structure appears to be, in many groups, more valuable than any other single character as a basis for classification, because more indicative of the general organisation of the animal. Examples of both these applications will be presently given.

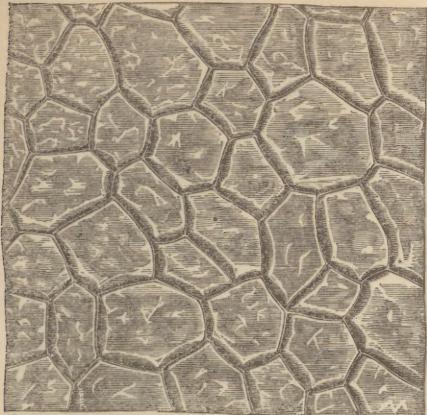
Mollusca.—The shells of Mollusca may always be regarded as *epidermic* in their character; being formed upon the surface of the mantle, which answers to the true skin of other animals. As might be anticipated from this description, they are essentially composed of *cells*, consolidated by a deposit of carbonate of lime in their interior; but, as in other tissues, we frequently find that the original cellular organisation is obscured by subsequent changes, and we sometimes lose all traces of it. We shall first examine it in what may be considered its typical condition, which is most characteristically seen in certain bivalves.

If a small portion be broken away from the thin margin of the shell of any species of *Pinna*, (this margin being composed of the outer layer only, which projects beyond the inner), and it be placed without any preparation under a low magnifying power, it presents on each of its surfaces, when viewed by transmitted light, very much the appearance of a honeycomb; whilst at the broken edge it exhibits an aspect which is evidently fibrous to the eye, but which, when examined under the microscope with reflected light, resembles that of an assemblage of basaltic columns. The shell is thus seen to be composed of a vast number of prisms, having a tolerably uniform size, and usually presenting an approach to the hexagonal shape. These are arranged perpendicularly (or nearly so) to the surface of the lamina of the shell; so that its thickness is formed by their length, and its two surfaces by their extremities. A more satisfactory view of these prisms is obtained by grinding down a lamina until it possesses a high degree of transparency; and it is then seen (fig. 407.) that the prisms themselves appear to be composed of a very homogeneous substance, but that they are separated by definite and strongly-marked lines of division. When such a lamina is submitted to the action of dilute acid, so as to dissolve away the carbonate of lime, a tolerably firm and consistent membrane is left, which exhibits the prismatic structure just as perfectly as did the original shell (fig. 408.); the hexagonal divisions being evidently the walls of cells resembling those of the pith or bark of a plant, in which the cells are frequently hexagonal prisms. In very thin natural laminae, the nuclei of the cells can often be plainly distinguished; but we cannot expect to find these, when the two ends of the cells (at one of which they are generally situated) have been removed by grinding. By making a section of the shell perpendicularly to its surface, we obtain a view of the prisms cut

in the direction of their length (fig. 409.) ; and it is then seen that whilst many of them pass

shells, that the decay of the animal membrane leaves the contained prisms without any con-

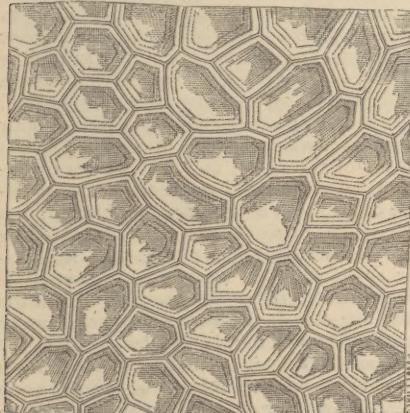
Fig. 407.



Section of the shell of *Pinna* parallel to the surface, showing prismatic cellular structure, cut transversely. Magnified 185 diameters.

continuously from one surface of the layer to the other, some terminate in points midway.

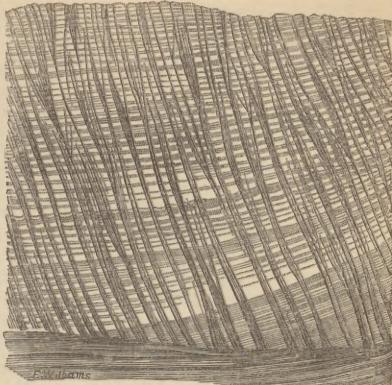
Fig. 408.



Lamina of decalcified membrane of prismatic cellular structure, from shell of *Pinna*. Magnified 185 diameters.

Hence it happens that the *number* of the reticulations is smaller on the interior than on the exterior of the layer ; their *size*, on the contrary, being greater. The prisms are seen to be marked by delicate transverse striae, closely resembling those observable on the prisms of the enamel of teeth, to which this kind of shell-structure may be considered as bearing a very close resemblance, except as regards the mineralising ingredient. If a similar section be decalcified by dilute acid, the membranous residuum will exhibit the walls of the prismatic cells viewed longitudinally ; and these will be seen to be more or less regularly marked by the transverse striae just alluded to. It sometimes happens in recent, but still more commonly in fossil

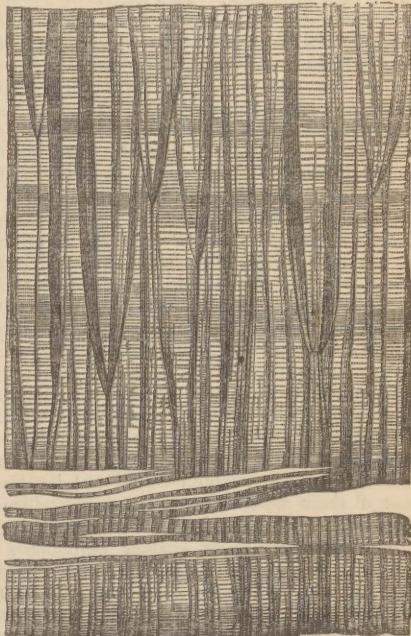
Fig. 409.



Vertical section of prismatic cellular structure, from external layer of shell of *Unio occidens*. Magnified 40 diameters.

necting medium ; and being then quite isolated, they can be easily detached from one

Fig. 410.



Vertical section of cellular structure of *Pinna* ; at its lower part the membrane is splitting into thin layers. Magnified 74 diameters.

another without any fracture. A group of three such prisms, found in a fragment of chalk, is shown in fig. 411. : it is seen that these also exhibit transverse striae of a similar aspect. By submitting the edges of the membranous walls of the prismatic cells divided longitudinally (as in fig. 410.) to a high magnifying power, the cause of the transverse

striation is seen to be a thickening of the cell-wall in those situations ; which will of course

thickness of the shell is made up of the internal or nacreous layer ; but a uniform stratum

Fig. 411.



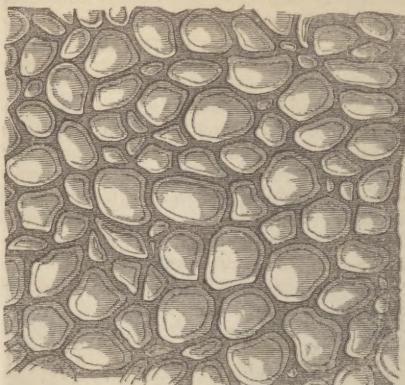
Calcareous prisms of the shell of *Pinna* ; from Chalk.

produce a corresponding series of indentations upon the contained prisms. This thickening seems best accounted for by supposing (as first suggested by Prof. Owen) that each long prismatic cell is made up by the coalescence of a pile of flat epidermic cells, the transverse striation marking their lines of junction ; and this view corresponds well with the fact that the shell-membrane not unfrequently shows a tendency to split into thin laminae along the lines of striation, as shown in the lower part of fig. 410. ; whilst we occasionally meet with an excessively thin natural lamina, composed of flat pavement-like cells resembling those of the epithelium of serous membrane, lying between the thicker prismatic layers, with one of which it would have probably coalesced but for some accidental cause which preserved its distinctness. That the entire length of the prism is not formed at once, but that it is progressively lengthened and consolidated at its lower extremity, would appear also from the fact that where the shell presents a deep colour (as in *Pinna nigrina*) this colour is usually disposed in distinct strata, the outer portion of each layer being the part most deeply tinged, whilst the inner extremities of the prisms are almost colourless.

The prismatic arrangement of the carbonate of lime in the shells of *Pinna* and its allies has been long familiar to conchologists ; but it has been usually regarded as the result of crystallisation. It is now, however, perfectly evident that the calcareous prisms are nothing else than *casts* of the interior of the prismatic cells ; the form of which, however irregular, they constantly present ; whilst the markings of the membrane are faithfully transferred to the surface of the prism. Further, the prisms in a thick layer of shell frequently present a decided curvature, which would not be the case if their form were due to crystallisation. Not unfrequently, moreover, they are altogether destitute of angular boundaries ; the large quantity of animal matter disposed between the contiguous cells giving them a rounded contour, as seen in fig. 412, and thus causing the calcareous casts of their interior to be cylindrical rather than prismatic.

It is only in a few families of Bivalves, however, that the cellular structure is seen in this very distinct form, or that it makes up a large part of the substance of the shell ; and these families are for the most part nearly allied to *Pinna*. In all the genera of the *Margaritaceæ*, we find the external layer of the shell formed upon this plan, and of considerable thickness ; the internal layer being nacreous. In the *Unionidæ*, on the contrary, nearly the whole

Fig. 412.



Lamina of outer layer of shell of *Ostrea edulis*, showing its cellular structure, with a large amount of intercellular substance. Magnified 250 diameters.

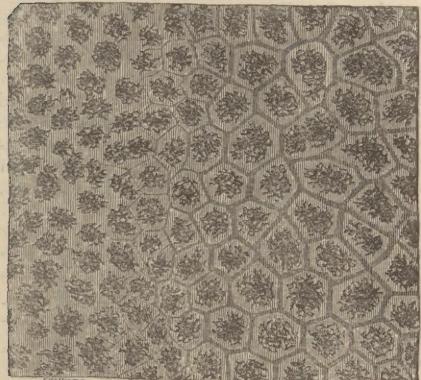
of prismatic cellular substance is always found between the nacre and the periostracum. In the *Ostraceæ* the greater part of the shell is composed of a sub-nacreous substance, the successively-formed laminae of which have very little adhesion to each other ; but every one of these laminae is bordered at its free edge by a layer of the prismatic cellular substance, distinguished by its brownish-yellow colour : this structure presents itself again in the family *Pandoridae*, which belongs to quite a different section of the class ; and it is curious to observe that the marked difference in the structure of the shells of *Pandora* and *Lyonia* from that of the *Anatinidæ* and other neighbouring families, harmonises completely with the peculiar combination of characters presented by the animals of these two genera.* In all the foregoing cases, a distinct cellulo-membranous residuum is left after the decalcification of the prismatic substance by dilute acid ; and this is most tenacious and substantial where, as in the *Margaritaceæ*, there is no proper periostracum, — as if the horny matter which would have otherwise gone to form this investment had been diffused as an intercellular substance between the proper cell-walls.

In many other instances, a cellular arrangement is perfectly evident in sections of the shell ; and yet no corresponding structure can be distinctly seen in the delicate membrane left after decalcification. In all such cases, the animal basis bears but a very small proportion to the calcareous deposit, and the shell is usually extremely hard. A very characteristic example of this is presented by the outer layers of the shells of the genus *Thracia* and other *Anatinidæ*. But there are numerous other cases, in which no traces of cellular structure can be detected in the fully-formed shell, and in which we can only be guided by analogy in

* See Forbes and Hanley's *British Mollusca*, vol. i. pp. 207, 213.

assigning to them a similar origin with the preceding. We seem justified in doing so, however, by two considerations. In the first place, where the fully-formed shell is destitute of cellular arrangement, this may be frequently detected in the embryonic shell ; as the author is informed by Dr. Leidy of Philadelphia, who has carefully studied the embryology of many Mollusca. And secondly, there are certain shells which exhibit so complete and gradual a transition from a distinct cellular arrangement to an apparently homogenous structure, that we can scarcely doubt the common origin of both substances. This is particularly well seen in the common *Mya arenaria*, a careful examination of which shell brings to light numerous interesting varieties of cellular organisation. Thus in *fig. 413.* we see in one part of

Fig. 413.

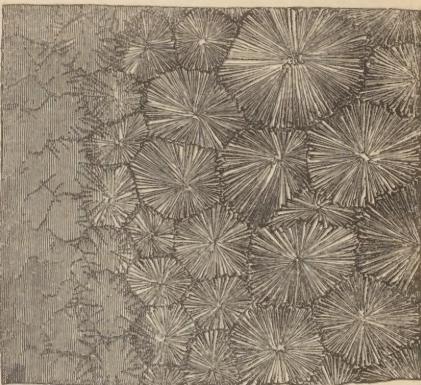


Section of shell of *Mya arenaria*, showing in one part distinct cellular partitions, with large nuclear spots ; whilst in another part of the same layer, the cell-boundaries become fainter, and then disappear altogether. Magnified 150 diameters.

the section a very distinct set of cell-boundaries, with a large nuclear spot in the centre of each cell ; whilst on the other side we observe that the cell-walls have completely disappeared,—the nuclear spots, however, still remaining to mark the cellular origin of the substance. A little further on, these also might disappear, and thus all traces of the original organisation might be lost, though no reasonable doubt could be entertained as to its prior existence. A very curious variety of cell-structure is seen in the large hinge-tooth of *Mya*, in which there is a layer of large cells occupied by carbonate of lime disposed in a radiated form of crystallisation, resembling that of the mineral called Wavellite. Approaches to this beautiful arrangement may be seen in many other shells. Here, too, we find the partitions between the cells gradually becoming less distinct, as we pass from this peculiar stratum into the surrounding substance, until we lose them altogether. In general, a cellular layer may be detected upon the external surface of bivalve shells, where this has been protected by a periostracum, or has been prevented in any other mode from undergoing abrasion :

thus it is found occasionally in *Anomia* and *Pecten*, and generally in *Chama*, *Cleidothærus*,

Fig. 414.



Section of the hinge-tooth of *Mya arenaria*, showing radiating arrangement of carbonate of lime within the cells, and the gradual disappearance of the cell-boundaries, so that the texture becomes homogeneous. Magnified 80 diameters.

Trigonia, *Anatina*, *Solen*, *Glycimeris*, *Solemya*, &c. In the last-named genus it is very firm, and leaves a distinct membranous residuum after the calcareous matter has been removed by acid, which is not the case with the others. The cells of which the outer layer of the shell is made up are frequently rather *fusiform* than prismatic in their shape, and are disposed with their long axes nearly parallel to its surface, so that their extremities "crop out" very obliquely on its exterior, where their rounded terminations, containing nuclei, may often be distinguished when the surface has not suffered abrasion. (See *fig. 416.*)

The internal layer of Bivalve shells rarely presents a distinct cellular structure, when examined in a thin section ; and the residuum left after decalcification is usually a distinct but structureless membrane, closely resembling the "basement membrane" of Mr. Bowman. (MUCOUS MEMBRANE.) This form of shell-substance may consequently be distinguished as *membranous*. In the *Margaritaceæ* and many other families, this internal layer has a nacreous or iridescent lustre, which depends (as Sir D. Brewster has shown*) upon the striation of its surface with a series of grooved lines, which usually run nearly parallel to each other. As these lines are not obliterated by any amount of polishing, it is evident that their presence depends upon something peculiar in the texture of this substance, and not upon any mere superficial arrangement. When a piece of nacre is carefully examined, it becomes evident that the lines are produced by the cropping-out of laminæ of shell situated more or less obliquely to the plane of the surface. The greater the *dip* of these laminæ, the closer will their edges be ; whilst the less the angle which they make with the surface,

* Phil. Trans. 1814.

the wider will be the interval between the lines. When the section passes for any distance in the plane of a lamina, no lines will present themselves on that space. And thus the appearance of a section of nacre is such as to have been aptly compared by Sir J. Herschel* to the surface of a smoothed deal board, in which the woody layers are cut perpendicularly to their surface in one part, and nearly in their plane in another. Sir D. Brewster appears to suppose† that nacre consists of a multitude of layers of carbonate of lime alternating with animal membrane; and that the presence of the grooved lines on the most highly-polished surface is due to the wearing away of the edges of the animal laminæ, whilst those of the hard calcareous laminæ stand out. If each line upon the nacreous surface, however, indicate a distinct layer of shell-substance, a very thin section of mother-of-pearl ought to contain many thousand laminæ, in accordance with the number of lines upon its surface; these being frequently no more than 1-7500th of an inch apart. But when the nacre is treated with dilute acid, so as to dissolve its calcareous portion, no such repetition of membranous layers is to be found: on the contrary, if the piece of nacre be the product of one act of shell-formation, there is but a single layer of membrane. The membrane is usually found to present a more or less *folded* or *plaited* arrangement; but this has generally been obviously disturbed by the disengagement of carbonic acid in the act of decalcification, which tends to unfold the plaits. There is one shell, however,—the well-known *Haliotis splendens*,—which affords us the opportunity of examining the plaits *in situ*, and thus presents a clear demonstration of the real structure of nacre. This shell is for the most part made up of a series of plates of animal matter, resembling tortoise-shell in its aspect, alternating with thin layers of nacre; and if a piece of it be submitted to the action of dilute acid, the calcareous portion of the nacreous layers being dissolved away, the plates of animal matter fall apart, each one carrying with it the membranous residuum of the layer of nacre that was applied to its inner surface. It will usually be found that the nacre-membrane covering some of these horny plates will remain in an undisturbed condition; and *their surfaces then exhibit their iridescent lustre*, although all the calcareous matter has been removed from their structure. On looking at the surface with reflected light under a magnifying power of 75 diameters, it is seen to present a series of folds or plaits more or less regular; and the iridescent hues which these exhibit are often of the most gorgeous description. But if the membrane be extended with a pair of needles, these plaits are unfolded, and it covers a much larger surface than before; and the iridescence is then completely destroyed. This experiment, then, demonstrates that the peculiar lineation of the surface of nacre (on which the iridescence undoubtedly

depends, as first shown by Sir D. Brewster) is due, not to the outcropping of alternate layers of membranous and calcareous matter, but to the disposition of a single membranous layer in folds or plaits, which lie more or less obliquely to the general surface.

There are several bivalve shells which present what may be termed a *sub-nacreous* structure, their polished surfaces being covered with lines indicative of folds in the basement membrane; but these folds are destitute of that regularity of arrangement which is necessary to produce the iridescent lustre. This is the case, for example, with most of the *Pectinidae*, also with some of the *Mytilaceæ*, and with the common *Oyster*. Where there is no indication of a regular corrugation of the shell-membrane, there is not the least approach to the nacreous aspect; and this is the case with the internal layer of by far the greater number of shells, the presence of nacre being exceptional, save in a small number of families.

The membranous shell-substance, some form of which constitutes the internal layer of most bivalve shells, is occasionally traversed by tubes, which seem to commence from the inner surface of the shell, and to pass towards the exterior. These tubes vary in size from about the 1-20,000th of an inch, or even less, to about the 1-2000th; but their general diameter, in the shells in which they most abound, is about 1-4000th of an inch. The direction and distribution of these tubes are extremely various in different genera. Thus, in *Anomia Ephippium* they are scarcely distributed in the internal nacreous lamina; but in the yellow outer layer they are very abundant (fig. 415.), forming an irregular net-work, which spreads out in a plane parallel to the surface. In *Cleidothærus chamoides*, on the other hand, the tubes are abundant in the internal layer of the nacreous lining, where they form an intricate but irregular net-work parallel to the internal surface of the shell; and from this arise a series of straight tubes, which pass nearly at right angles with the surface, at a considerable distance from each other, through the external portion of the nacreous layer, towards the cellular structure which constitutes the exterior of the shell. This, however, they do not penetrate; stopping short as they approach it, just as the tubes of dentine cease at its plane of junction with the enamel. The diameter of the tubes is tolerably uniform, even when they divaricate; the trunk not being much larger than either of the branches. In other instances, however, no such net-work is formed, but the tubes run at a distance from each other, traversing the shelly layers obliquely, and are then usually of comparatively large size: this is the case, for example, with some species of *Arca* and *Pectunculus*. That these tubes are not mere channels or excavations in the shell-substance, is proved by the fact that they may be frequently seen very distinctly in the decalcified shell-membrane. They often present, in their beaded aspect, indications of a cellular origin, as if they had been formed

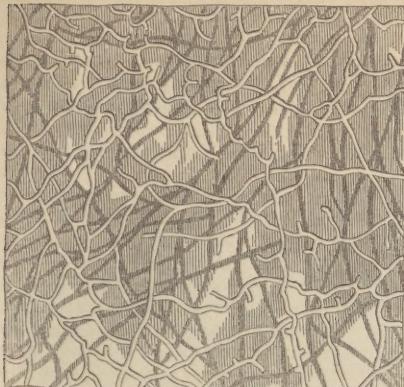
* Edinb. Philos. Journ. vol. ii.

† Loc. cit.

by the coalescence of a series of cells arranged in a linear direction. They are generally

everywhere a similar origin; and if one variety of membranous shell-substance be thus

Fig. 415.

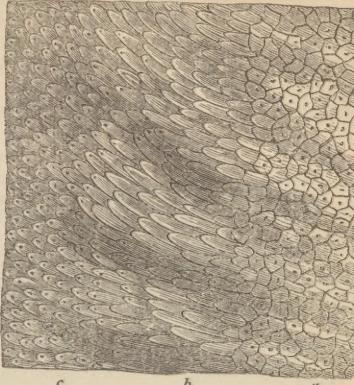


Tubular shell-structure from external surface of *Anomia Ephippium*. Magnified 250 diameters.

most abundant in shells whose exterior has a foliated or sculptured character; and not unfrequently they may be distinctly seen to pass directly towards the prominences of the surface, — as in *Lima scabra* and various species of *Chama*. They are by no means restricted, however, to shells thus characterised; nor are they universally present in them.

Of the origin and mode of formation of the membranous shell-structure, it is rather difficult to give an exact account. Possibly, after the epidermic cells have undergone calcification, so as to form the external cellular layer, the basement membrane itself may become detached from the surface of the mantle, in combination with a layer of calcareous matter. Even in nacre, however, which may be considered as the most perfect form of this substance, indications of cellular structure are not unfrequently to be seen, especially in univalve shells: these are particularly evident in *Haliothis*, the nacreous laminæ of which, when carefully examined under a sufficiently high magnifying power, are found to be composed of minute cells of a long oval form (fig. 416.), their short diameter not being above 1-5000th of an inch. Their boundaries in many parts are very indistinct, or even disappear altogether, so that every gradation can be traced, from the obviously cellular arrangement shown in fig. 412., to the homogeneous aspect presented by the nacre of bivalve shells. The same cellular structure, and the same gradation to a homogeneous stratum, may be made apparent in the decalcified membrane; so that here we seem to have evidence that even the membranous shell-substance is originally formed by the agency of cells, although the boundaries of these have usually been subsequently obliterated, so that the structure comes to present a homogeneous aspect. Indications of the same cellular organisation may be detected in the nacreous lining of the shell in *Turbo* and *Nautilus*. We seem justified in concluding that nacre

Fig. 416.



Cellular structure of nacre of *Haliothis splendens*: the cells cut transversely at *a*, longitudinally at *b*, and showing their terminations (with nuclear spots) at *c*. Magnified 450 diameters.

proved to have been formed by the agency of cells, little doubt can be entertained as to the corresponding organisation of others. The fact may probably be, that, as maintained by Professor Goodsir *, the basement membrane is itself composed of cells more or less perfectly developed, the boundaries of which usually disappear. Of this view a very good illustration is afforded by the various examples of shell-membrane; which present every gradation, from the most perfectly homogeneous pellicle, to a distinct stratum of cells.

The loss of the original boundaries of the cells, and the consequent obscuration of the real nature of the structure, are by no means peculiar to shell; for the physiologist is familiar with this change as occurring in various other tissues. Thus, in dentine, the cases in which the vestiges of the original cells are preserved are few in proportion to those in which they are obliterated; and yet these isolated examples are sufficient to mark the real nature of the transformation of the soft dentinal pulp into the dense ivory. It would seem as if, in the process of calcification, the cell-walls have a tendency to liquefy or dissolve away, unless supported by additional deposits of animal matter, thus allowing the complete fusion of their contents. The peculiar tenacity of the decalcified shell-substance in the *Margaritaceæ* and certain other tribes seems due, not so much to the strength of the original cell-walls, as to the interposition of an intercellular substance between them. In *Perna* we not unfrequently find, between the calcified layers, membranous laminæ consisting chiefly of horny matter interposed between rounded cells that are more or less widely separated from each other: here the animal substance

* Anatomical and Pathological Observations, p. 3, note.

would seem to be peculiarly abundant, being apparently of the same kind as that of which the *byssus* of these animals is composed.

The ordinary account of the mode of growth of the shells of Bivalve Mollusca,—that they are progressively enlarged by the deposition of new laminae, each of which is in contact with the internal surface of the preceding, and extends beyond it,—does not express the

whole truth; for it takes no account of the fact that most shells are composed of two layers of very different texture, and does not specify whether *both* these layers are thus formed by the entire surface of the mantle whenever the shell has to be extended, or whether only *one* is produced. An examination of *fig. 417.* will clearly show the mode in which the operation is effected. This figure

Fig. 417.



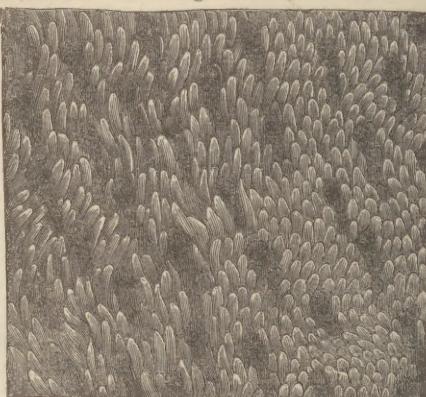
Vertical section of shell of Unio occidens, near the lip, showing the arrangement of the outer or prismatic, and the internal or nacreous layers: a a', b b', c c', successive lines of growth; d, margin of the valve. Magnified 8 diameters.

represents a section of one of the valves of *Unio occidens*, taken perpendicularly to its surface, and passing from the margin (at the right hand of the figure) towards the umbo (which would be at some distance beyond the left). This section brings into view the two substances of which the shell is composed; traversing the outer or prismatic layer in the direction of the length of its cells, and passing through the nacreous lining, which is seen to be made up of numerous laminae, separated by the lines *aa'*, *bb'*, *cc'*, &c. These lines evidently indicate the successive formations of this layer; and it may be easily shown, by tracing them towards the umbo on the one side, and towards the margin on the other, that at every enlargement of the shell its whole interior is lined by a new nacreous lamina, in immediate contact with that which preceded it. The number of such laminae, therefore, in the oldest part of the shell, indicates the number of enlargements which it has undergone. The outer or prismatic layer of the growing shell, on the other hand, is only formed where the new structure projects beyond the margin of the old; and thus we do not find one layer of it overlapping another, except at the lines of junction of two distinct formations. When the shell has attained its full dimensions, however, new laminae of both layers still continue to be added; and thus the lip becomes thickened by successive formations of prismatic structure, each being applied to the inner surface of the preceding, instead of to its free margin. The same arrangement may be well seen in the *Oyster*; with this difference, that the successive layers have but a comparatively slight adhesion to each other.

The shells of *Terebratulae*, and of several

other genera of *Brachiopoda*, or *Palliobranchiate* Bivalves, are distinguished by peculiarities of structure, which serve to distinguish them from all others. When thin sections of them are microscopically examined, they present a very peculiar texture, (*fig. 418. a.*)

Fig. 418.



Portion of the shell of Terebratula australis, showing the orifices of the perforations, and the peculiar structure of the shell: at a the shell is traversed by the section; at b is shown its internal surface.

which might be referred either to long flattened cells, or to plications in the shell-membrane; on the other hand, the natural internal surface of these shells always exhibits an imbricated aspect of great regularity (*b*). If the section pass very obliquely towards this surface, it becomes evident that these imbrications are formed by the outcrop of the long flattened cells or folds, which were seen when the plane of the section has passed in the direction of

their length. A great variety of appearances is presented by this structure, according to the direction in which it happens to be traversed by the section; but they are all indicative of its peculiar character, which is readily recognisable even in the minutest fragment, although its nature yet remains doubtful. The cells, if cells they be, must be excessively flattened; and no vestige of them can be traced in the decalcified shell; whilst, on the other hand, the membranous residuum does not give any distinct indication of having been plicated with the regularity necessary to produce such a remarkable appearance. When any recent species of *Terebratula* is examined, save *Ter. psittacea* (which is now generally excluded from the genus on other grounds), an additional peculiarity is observed; consisting of the presence of a large number of *perforations* in the shell, generally passing obliquely from one surface to the other, and terminating internally by an open orifice (fig. 418.), whilst on the exterior they are covered in by the *periostracum*. Their diameter, which is greatest towards the external surface, varies in different species from about 1-1800th to 1-500th of an inch; and there is a considerable difference, also, in their degree of proximity to each other. In some fossil species, as *Ter. bullata*, the interval between the passages is scarcely greater than the diameter of the passages themselves. When a portion of one of these shells, which has been preserved with the animal in spirit, has been completely decalcified by the action of dilute acid, the membranous residuum presents a very remarkable structure, no vestige of which is seen in the ordinary bivalves. Attached to the membranous films are a series of tubular appendages, corresponding in diameter to the perforations of the shell, and arranged at the same distances (fig. 419.): the free extremi-

contents are distinctly cellular, resembling the cells in the interior of glandular follicles. These *cœcal tubuli* lie in the perforations of the shell, and open on its inner surface; but there does not appear to be any system of tubes or canals for collecting the matter poured out from them, each *cœcum* having its distinct and independent termination on the internal surface of the shell. The surface of the mantle in contact with the shell is found to be studded with minute cells, corresponding in size and aspect with those contained in the *cœcal tubuli*. The physiological purpose of this curious structure is at present a mystery; but there can be little doubt that it is a very important one in the economy of the animal, when we see the shell thus rendered subservient to the special protection of the *cœcal appendages*. The perforations are wanting in a large proportion of the very numerous species of fossil *Terebratula*; and there would appear strong reason for regarding their presence or absence as a character of fundamental importance in the subdivision of this important genus.* In most of the non-perforated species, the shell is readily divisible into thin micaceous plates, which exhibit the characteristic texture of the shell in great perfection; and as this texture undergoes remarkably little change in the act of fossilisation, it is often possible to recognise a *Terebratula* from a very minute fragment, imbedded even in the palæozoic strata. A very similar structure exists in several genera allied to *Terebratula*; and in some of these, also, as *Orthis* and *Spirifer*, the distinction has to be established between the perforated and non-perforated species; whilst in *Atrypa* (to which the recent *Ter. psittacea* properly belongs), all the species are destitute of perforations.

There is not, by any means, the same amount of diversity in the structure of the shell in the class of *Gasteropoda*, as that which exists among the several tribes of *Conchifera*; a certain typical plan of construction being common to by far the greater number of them. The small proportion of animal matter contained in most of these shells is a very marked feature in their character; and it serves to render other features indistinct, since the residuum left after the removal of the calcareous matter is usually so imperfect, as to give no clue whatever to the explanation of the appearances shown by sections. Nevertheless, the structure of these shells is by no means homogeneous, but always exhibits indications, more or less clear, of an original organic arrangement. The porcellaneous shells, as formerly stated (vol. ii. p. 384), are composed of three layers, all presenting the same kind of structure, but each differing from the others in the mode in which this is arranged. This structure was described by Mr. Gray † as the result of rhomboidal crystallisation; each layer being com-

Fig. 419.



Decalcified membrane of shell of *Terebratula australis*, showing the cœcal tubuli, which occupy the perforations of the shell: the tubuli are filled with minute cells. Magnified 150 diameters.

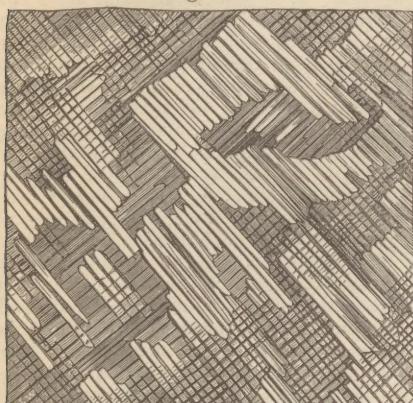
ties of these appendages have distinct cœcal terminations; and when a sufficient magnifying power is employed, it is found that their

* See a Paper on the Subdivision of the Genus *Terebratula*, by Mr. J. Morris, in the Journal of the Geological Society, vol. ii. p. 382.

† Phil. Trans. 1833, p. 790.

posed of thin laminæ placed side by side, which separate from one another in the planes of cleavage when the shell is fractured. As first pointed out, however, by Mr. Bowerbank, each of these laminæ really consists of a series of cells in close apposition; and the plates are disposed alternately in contrary directions, so that each series of cells intersects the one beneath it nearly at right angles, as seen in fig. 420. Although the intimate structure of

Fig. 420.



Portion of fractured surface of middle layer of *Cypraea mauritiana*, showing laminae composed of prismatic cells obliquely crossing one another. Magnified 235 diameters. (After: Bowerbank.)

each of the three layers of the shell is essentially the same, yet the disposition of the laminæ is not the same in any two adjoining ones,—an arrangement which adds greatly to the strength of the shell. The planes of the laminæ are always as nearly as possible either parallel or at right angles to the lines of growth; those of the inner and outer layers always having the same direction with each other, but those of the middle layer being set at right angles to them. When, therefore, a section is made parallel to the surface of the shell, it will cut the edges of the laminæ of which the layers traversed by it are composed; but if the section be made in a direction perpendicular to the surface, and pass through the middle layer in the plane of its laminæ, it will cut through the edges of the laminæ making up the interior and exterior layers; whilst if the section traverse the two latter in the plane of their laminæ, it will cut across the laminæ of the middle layer.

The principal departures from this plan of structure are seen in *Patella*, *Chiton*, *Halotis*, and *Turbo* and its allies. In *Patella*, the inner and outer layers are composed of large and irregular laminæ, by no means firmly adherent to one another; but the middle layer is made up of tolerably regular polygonal cells, which form only a thin stratum in some parts, whilst in others they are elongated into prismatic cells; and the directions of the laminæ, of which the inner and outer layers are composed, instead of

being conformable with each other, are at right angles. In *Chiton*, the external layer, which seems to be of a delicate fibrous texture, but which is of extreme density, is perforated by large canals, which pass down obliquely into its substance, without penetrating, however, as far as the middle layer. The middle layer, as in *Patella*, is distinctly cellular; whilst the internal has the same nearly-homogeneous texture as the external, but shows no trace of perforations. The peculiarities of structure presented by *Halotis* have been already described. In *Turbo* and its allies, the inner layer is nacreous, and the middle one is made up of large cells: the cellular structure is also very evident in the solid operculum of *Turbo*, when reduced to sufficient thinness.

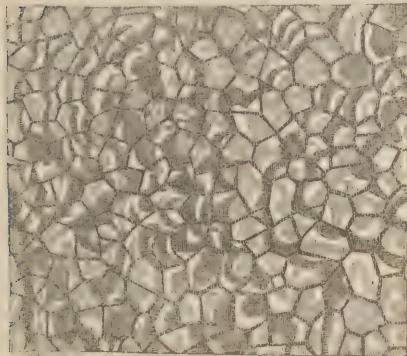
That the shell-substance in Gasteropoda is formed in the first instance by the agency of cells, however indistinct their traces may subsequently become, is further apparent from the researches of Mr. Bowerbank on the growth of the shell of the common garden-snail (*Helix aspersa*); and his observations further confirm the opinion already expressed, that the formation of each layer of shell is a progressive operation; new matter being added to its interior after the exterior has been consolidated.

Passing by the *Pteropoda*, whose delicate membranous shells present no very distinct structure, we come to the testaceous *Cephalopoda*, of which there are but few species now existing. The shell of *Nautilus pompilius* bears more resemblance to that of bivalves in its intimate structure, than to that of the Gasteropodous univalves; the three layers of perpendicular laminæ, so characteristic of the latter, not making their appearance here; and of the two layers of which the shell is composed, the inner one being nacreous, whilst the outer one is made up of an aggregation of cells of various sizes, those which are nearest the external surface being generally the largest. In the thin shell of *Argonauta*, the same kind of irregular cellular structure can be easily distinguished, as in the outer layer of the shell of *Nautilus*; but there would seem to be nothing comparable to the inner layer of the latter. The shell of *Spirula* must be considered to bear a greater resemblance, as regards its relation to the animal, to the *Sepiostaire* of the Cuttle-fish, than to the chambered shell of the *Nautilus*; although it so closely approximates the latter in its own conformation. This being the case, it is interesting to find that the intimate structure of the shell has a much greater resemblance to the *Sepiostaire* than would be supposed from its general aspect. For although its texture seems uniform, and its minute parts are composed of an aggregation of calcified cells, yet its surface is marked by sinuous lines, closely resembling those which are seen upon the transverse plates of the *Sepiostaire*; and these lines or bands project in such a degree, that they might be considered as rudiments of the vertical partitions

which connect these plates. The *Septostaire* having been formerly described in some detail (vol. i., p. 546), it will only be requisite here to mention, that the calcified layers which alternate with horny membranes to form the shallow cone or cup, exhibit a distinct cellular structure, when the section is made sufficiently thin; and that indications of a similar structure may also be perceived in the delicate and fragile plates which are arranged obliquely upon one another in the hollow of this cup. Few of the numerous fossil shells referable to this class have yet been examined; it may, however, be stated as an interesting result of microscopic observation, that the "spathose guard" of the *Belemnite* is thereby proved to be composed of long prismatic cells, radiating from the centre to the circumference; closely resembling in their general arrangement those of the massive tube of *Septaria gigantea*, the great sand-boring *Teredo* of Sumatra.

The structure of the shells of the testaceous *Annelida*, and of the pedunculate *Cirrhopoda*, does not essentially differ from that of *Mollusca*; but in most of the sessile *Cirrhopoda*, such as the common *Balanus*, we find a *cancellated* structure or diploë intervening between the inner and outer plates of the shell (vol. i., p. 685). A less regular

Fig. 421.



Cancellated structure from shell of *Hippurite*, as seen in transverse section. Magnified 5 diameters.

diploë has been described by Mr. J. E. Gray* as existing between the laminae of *Ostrea purpurea*; but in no other shells of existing *Mollusca* has any approach to it been yet discovered. A very regular cancellated structure, however, is exhibited in the singular extinct group of *Rudistes*, where it makes up nearly the entire thickness of the shell (fig. 421.). The cancelli are usually short hexagonal prisms, terminated at each end by a flat partition; consequently, a section taken in one direction (fig. 421.) will exhibit the walls of the chambers disposed in a hexagonal network; whilst a section that passes at right angles to this will bring into view the trans-

verse partitions (fig. 422.). The cancelli are frequently occupied by calcareous infiltration.

Fig. 422.



Cancellated structure from the shell of *Hippurite*, as seen in vertical section. Magnified 5 diameters.

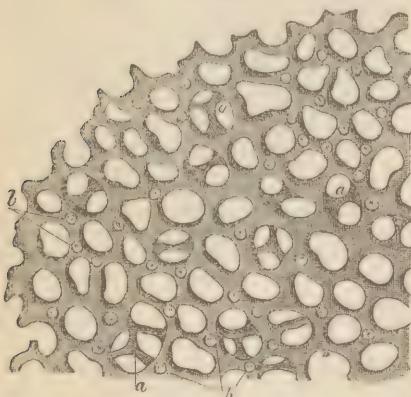
tion; which might lead to the belief that, like the cells of the *Pinna*, they were so consolidated in the living state. But they are also to be met with entirely empty, or with their walls merely lined by calcareous crystals; so that there can be no doubt that they were originally hollow. The presence of this structure assists in determining the zoological position of the curious group in question, which many considerations would lead us to regard as having been intermediate between the Bivalve *Mollusca* and the sessile *Cirrhopoda*. And it may be added that, by the same evidence, the place of the curious *Pleurorhyncus hibernicus*, a fossil which has been assigned to a different tribe by almost every naturalist who has examined it, would unhesitatingly be determined as amongst the *Rudistes*.

Echinodermata.—The structure of the skeleton in this class is entirely different from that which we have found to be characteristic of the *Mollusca*; whilst, in its essential features, it presents a remarkable uniformity throughout the various members of the group. The general arrangement of its components is the same, for example, in the firm plates which make up the testa of the *Echinida*, in the joints of the stems and branches of the *Crinoidea*, and in the scattered calcareous deposits which are met with in the integuments and in the tentacula of the *Holothurida*.

The elementary structure of the skeleton of the *Echinodermata* may be described as a *net-work*, composed of calcareous and animal matter intimately united; the former, however, being greatly predominant. In this net-work, the interspaces or *areolæ*, and the solid structure which surrounds them, may bear an extremely variable proportion to one another; so that, in two masses of equal size, the one or the other may greatly pre-

dominate, and the texture may have either a remarkable lightness and porosity, or a considerable degree of compactness and brittleness. We may take the plates making up the shell of the Echinus as presenting a typical form of this structure; from which the transition is easy towards either the more solid or the more open character which it elsewhere presents. When we obtain a very thin slice of one of these plates, taken parallel to the surface of the shell, we find that it is composed of a lamina, apparently in itself destitute of structure, perforated with considerable regularity by apertures of a circular or oval form. The diameter of these apertures (fig. 423.) varies to a certain extent in

Fig. 423.



Thin Lamina of shell of *Echinus*, showing its areolar structure: *aa*, portions of subjacent layer; *bb*, fractured bases of columns connecting the superposed laminae. *Magnified 164 diameters.*

different parts of the same shell, the reticulation being much coarser in the inner than in the outer layers: from numerous measurements, the extremes may be stated at about 1-450th and 1-2500th of an inch. The entire thickness of the shell is made up of an immense number of such plates, which lie parallel to each other, but not in contact; for they are separated from each other by little pillars, which rise up vertically from each plate to support the next, and which thus connect the different plates whilst holding them apart. The broken bases or ends of these minute pillars are commonly to be seen upon the surfaces of the perforated plates, at the spots intermediate between three or four of the apertures (fig. 423. *b, b*). The successive plates are always so disposed, that the centres of the perforations of one shall correspond with the intermediate solid structure of the next (fig. 423. *a, a*); and their transparency is such, that, when we have reduced a section to such a degree of thinness as to contain a small number of the reticulated layers, it is easy, by a proper adjustment of the focus of the microscope, to bring either one of them into distinct view. In whatever direction we slice the shell of the

Echinus, we always meet with a sort of reticulated structure; for if our section be parallel to the surface of the plates, it brings into view one or more of the perforated laminae just described; whilst, if it be perpendicular to the surface, it passes vertically through a series of these laminae, and in the direction of the pillars that connect them, which thus constitute an areolar structure of a tolerably regular form. The testa is thus of an extremely porous character, the areolæ having the freest communication with each other. Even in the living state, however, the areolæ appear to be empty, the ingress of the fluid with which the surface of the shell is in contact being prevented by the delicate membrane that covers it. At the same time, it possesses a remarkable degree of strength, in proportion to the amount of solid matter employed in its construction; for every part at the same time supports, and is supported, by the surrounding fabric.

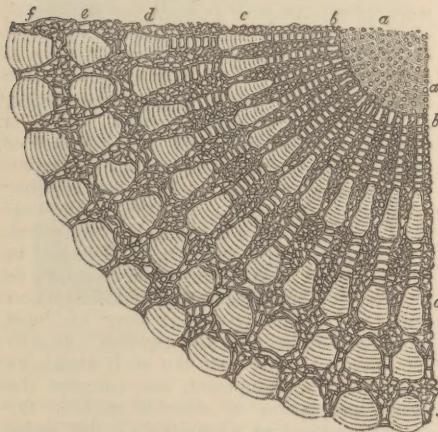
The skeleton of the Echinodermata contains very little organic matter. When it is submitted to the action of dilute acid, so that the calcareous matter is removed, the residuum is very small in amount; indeed, unless the acid be so weak as *only just* to dissolve the carbonate of lime, the organic matter also will be dissolved, and no animal basis will be apparent. When, however, it is obtained in a state fit for examination, it is found to possess the reticular structure of the calcareous shell; the meshes or areolæ being bounded by a substance in which a fibrous appearance, intermingled with granules, may be discerned under a sufficiently high magnifying power, as was first pointed out by Professor Valentin. This tissue bears a close resemblance to the areolar tissue of higher animals; and the shell may probably be considered as formed, not by the consolidation of the cells of the epidermis, as in the *Mollusca*, but by the calcification of the fibro-areolar tissue of the true skin. This calcification of areolar or simply fibrous tissue, by the deposit of mineral substance, not in the meshes of areole, but in intimate union with the organic basis, is a condition of much interest to the physiologist; for it presents us with an example, even in this low grade of the animal kingdom, of a process which seems to have an important share in the formation and growth of bone, viz. the progressive calcification of the fibrous tissue of the periosteum.*

Not only the entire shell, but the framework by which the teeth of the Echinus are enclosed and supported, is composed of a calcareous reticulation similar to that now described; nor is it confined to these solid structures. It has been pointed out by Professor Valentin, that the buccal membrane contains isolated patches of extreme delicacy; and the same eminent observer has detected a most beautiful example of this

* See Dr. Sharpey's Introduction to the Fifth Edition of Dr. Quain's Anatomy, p. 148, *et seq.*

structure in the calcareous rosette, with which, as long since observed by Monroe, the sucker at the extremity of each ambulacral tube is furnished. But it is in the spines with which the shell is beset, that the most remarkable displays of it are to be met with ; for it is there disposed in connection with solid ribs or pillars, which increase the strength of these organs, in such a manner as to constitute a most regular and elaborate pattern, which appears to differ in every distinct species. When we make a thin transverse section of almost any spine belonging to the genus *Echinus*, we are at once made aware of the existence of a number of concentric layers, arranged in a manner that strongly reminds us of the layers of wood in the stem of an exogenous tree. The number of these layers is extremely variable ; depending, not merely upon the age of the spine, but upon the part of its length from which the section is taken. The centre of the spine (fig. 424. a.) is filled up

Fig. 424.



Transverse section of spine of *Echinus* : a, medullary centre ; bb, first layer of solid pillars ; cc, dd, ee, ff, successive rings of growth. Magnified 45 diameters.

with the same kind of calcareous net-work as that of which the shell is composed ; and this is sometimes so delicate, as to appear as if made up by the interlacement of mere threads. This medullary centre is bounded by a row, more or less circular according to the form of the spine (which is sometimes angular), of open spots (b, b, b), in which it is deficient : these, on a cursory inspection, might be supposed, from their transparency, to be void spaces ; but a closer inspection makes it evident that they are the sections of a circular row of solid ribs or pillars, which form the exterior of every layer. Their solidity becomes very obvious when we either examine a section of a spine whose substance is pervaded (as frequently happens) with a deep colour, or when we look at a thin section of any spine by polarised light. Around the first circle of these solid pillars,

we find another layer of the fibro-calcareous net-work, which again is bounded by another circle of solid pillars, whose transverse sections are seen at c, c, c. The same arrangement may be repeated many times, (d, e, e). On looking at the outer border of the section, we observe that the rounded sides of these pillars (f, f) form a series of projections with hollows between them ; and these exactly correspond with the projecting ribs and furrows which we may notice running along the natural surface of the spine when we examine this with a magnifying glass, or even (in some instances) with the naked eye.

Although there is nothing like interstitial growth in the shell or spines of the *Echinus*, yet both are progressively enlarged by the addition of new matter. The polygonal plates of which the shell is composed are separated from each other by a membrane that passes into every suture ; and the margins of each plate appear to receive periodical additions, by calcareous deposit in the substance of this membrane. In this manner the globular form of the entire shell is preserved, whilst it undergoes progressive enlargement ; new plates being added, as they may be required, round the anal orifice of the shell (Agassiz). There can be little doubt that the spines are, in like manner, periodically augmented in diameter by successive formations or acts of growth, which take place in the investing membrane ; and a longitudinal section of the spine makes it evident that these additions not only surround the preceding deposits from the base upwards, but pass considerably beyond them, thus adding to the length of the spine. The consequence is, that a transverse section taken near the base of the spine will exhibit all the layers of which it is made up, each layer being narrow, and the central medulla small. A section taken at about the middle of the length may very probably not cut across the original spine nor the older layers, which do not reach so far ; and a section taken across the spine near its apex will only traverse the one or two layers last formed. Nevertheless, in many species, the spine is larger at that part than near its base ; but the large size is due to the great expansion of the medullary centre, which is composed of a very loose calcareous reticulation.

The structure of the shell of the *Echinus* is repeated in that of the three genera which may be regarded as the types of the principal subdivisions of the order *Echinida*, — namely, *Cidaris*, *Clypeaster*, and *Spatangus* : there can be no reasonable doubt, therefore, that it is universal throughout the group. The spines, however, of *Cidaris*, present a marked variation from the plan of structure exhibited in *Echinus* ; for they are usually nearly cylindrical in form, destitute of concentric layers, and composed of a calcareous reticulation enveloped in a cylinder of a solid, apparently homogeneous substance, chiefly calcareous,

which rises up in ridges upon the exterior. Hence it would appear that, like endogenous trees, whatever additions these spines may receive in length, they can receive little or none in diameter. The slender, almost filamentary species of the *Spatangaceæ*, and the innumerable minute hair-like processes attached to the shell of the *Clypeasteridae*, are composed of a like regular reticulated tissue; many of these are extremely beautiful objects when examined with the microscope without any preparation. It is interesting also to remark, that the same structure presents itself in the *Pedicellariae*, which are found upon the surface of many *Echinidae*, and which have been so great a source of perplexity to naturalists. The complete conformity which exists between the structure of their skeleton, and that of the animal to which they are attached, would seem to remove all reasonable doubt that they are truly appendages to it; as their actions also would indicate.

The same structure presents itself in the calcareous plates which form the less perfect skeletons of the *Asteriidae*, and also in their spines, when these (as in the large *Goniaster equestris*) are furnished with a calcareous frame-work, and are not mere projections of the hard integument. It is also met with in the family *Ophiuridae*, which forms, in some respects, the transition to the Crinoidal group; but the calcareous skeleton is here generally subordinate to the firm and almost horny integument. In the *Crinoidea*, on the other hand, the calcareous skeleton is highly developed, and its structure is extremely characteristic. This is well displayed in the recent *Pentacrinus Caput Medusæ*, the stem and branches of which are made up of a calcareous net-work, closely resembling that of the shell of the *Echinus*. There is exhibited, moreover, in a transverse section of the stem of *Pentacrinus*, as in the spines of *Echinus*, a certain regular pattern, which results from the varying dimensions of the areolæ in different parts. This pattern, formed by the extension of five pairs of rays (strongly reminding us of the medullary rays of plants) from the centre towards the circumference, is frequently well preserved in the fossilized stems of *Pentacrini*, and varies in different species sufficiently to serve as a distinctive character. In the round-stemmed *Encrinites*, a transverse section of the joints exhibits a simple concentric arrangement.

It only remains for us to notice the order *Holothuridae*, in which, as is well known, the calcareous skeleton of the other *Echinodermata* is reduced to its most rudimentary condition; never forming a complete and connected framework, but only showing itself in detached pieces, the disposition of which is extremely variable. In the typical *Holothuria*, there are five solid calcareous plates around the mouth, in which the calcareous reticulation is very characteristically seen. Each of the tentacula, also, has a small calcareous disk at its extremity, which presents a sort of rude sketch of the beautiful struc-

ture of the rosette that supports the ambulacratal suckers of the *Echinus*.

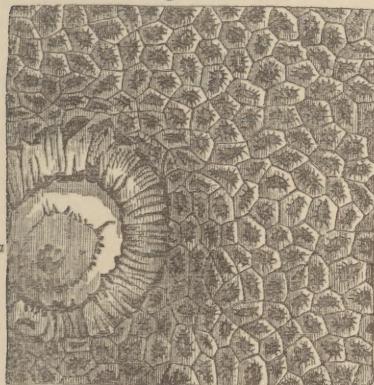
There can be no reasonable doubt that this peculiar arrangement is universal throughout the group, since it has been detected in characteristic examples of every one of its principal subdivisions. And, consequently, as no similar calcareous reticulation is found in the internal or external skeleton of any other animal, even the minutest fragment which distinctly presents this structure may be referred with certainty to an *Echinoderm*. And this structure is perfectly preserved, even after the substance has been infiltrated with calcareous matter in the act of fossilization, and has become so completely mineralised, that the disposition to rhomboidal fracture makes it difficult to obtain a section in any other direction than that of the plane of cleavage. As already remarked, the elementary structure is essentially the same everywhere; so that it might not be possible to determine from a very minute fragment whether it formed part of the shell of an *Echinus*, *Cidaris*, or *Spatangus*, — a portion of the framework of an *Asterias*, *Ophiura*, or *Holothuria*, — or entered into the composition of the stem of an *Encrinite*. But where any regular pattern is displayed, this is frequently sufficient to distinguish the genus, or even the species, to which the fragment belonged. This is certainly the case in regard to the spines of *Cidaris* and the stems of *Pentacrinites*; and will probably be found no less true in other instances, when these beautiful structures shall have been more extensively investigated.

Crustacea. — The structure of the shell in *Crustacea* has been hitherto examined only in the Decapod order; and that of the common crab (*Platycarcinus pagurus*) alone has been subjected to a minute investigation. It is in the Decapod order that the shell attains its most perfect development, and contains the largest proportion of mineral matter: the special respiratory apparatus in this order being so elaborate as to render unnecessary any participation of the general tegumentary surface in the function of respiration. (See vol. i. p. 752.)

The shell of the Decapod *Crustacea* consists of three layers; — namely, 1. a horny epidermic membrane covering the exterior; 2. a cellular or pigmentary stratum; and 3. a calcareous or tubular substance. The horny epidermic membrane is easily detached from the subjacent layers, after the shell has been immersed for a time in dilute acid; it is thin but tenacious, presenting no trace of structure, though it may exhibit markings on the under surface, derived from its contact with the cellular layer beneath. The pigmentary stratum is very thin in the crab and lobster; but in some other Decapods it is much thicker. In *Scyllurus latus*, it is stated by M. Lavalley to be the thickest of the three layers of the shell; and in the cray-fish and many other species, according to the same observer, it seems made up of a considerable number of layers, its vertical section being traversed by several ex-

tremely fine lines, passing in a direction parallel to the surface of the shell and to each other. The number of these is usually from six to fifteen; but they sometimes amount to as many as thirty, or even sixty, their number not being in relation either to the thickness of the pigmentary layer, nor to the size of the species observed; but appearing to augment with age. The cellular layer is that in which the colouring matter of the shell is solely contained; but it does not always contain pigment, its structure being precisely the same on the white under-surface of the crab as on the reddest portion of its carapace. When examined with a low magnifying power, it presents an areolar aspect; but when a sufficiently thin section is viewed by transmitted light with a high magnifying power, the character of the net-work, and of the dark spaces it encloses, becomes at once apparent. It is

Fig. 425.



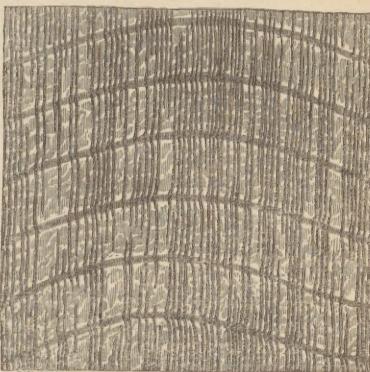
Cells of pigmentary layer of shell of Crab; *a*, papillary elevation of subjacent layer. Magnified 400 diameters.

then obvious that the nearly colourless polygonal reticulations are the thickened walls of cells, each of them being divided by a distinct line, which marks the junction of the contiguous boundaries; whilst the dark spaces or areolæ are the cavities of the cells, filled with colouring matter, or with some other semi-opaque substance. This cellular layer is not uniformly disposed over the entire surface of the crab-shell; for the calcareous layer beneath rises up through it in little papillary elevations (fig. 425. *a*), to the summit of which the epidermis adheres. It is from the deficiency of the pigmentary layer at these points, that the shell derives its minutely speckled appearance.

The internal layer is that which constitutes by far the thickest part of the shell of the crab, and which must be regarded as its fundamental or essential element, since (according to M. Lavalle) it is never wanting in the Decapod Crustacea, whilst other layers are sometimes deficient. It is in this internal layer, that the calcareous matter is chiefly deposited; but even after this has been removed, a very distinct animal basis is left,

possessing considerable firmness, and closely resembling that which is left after the decalcification of dentine. When a thin section of it is made parallel to its surface, and subjected to a high magnifying power, it is seen to be composed of an apparently homogeneous substance, studded with minute points, each surrounded by a clear space, which correspond with those seen in a section of dentine cut at right angles to the course of its tubuli, and which would seem to possess the same essential character with them. A thin section of the shell taken in the opposite direction (*i. e.* from surface to surface) leaves no doubt, when examined with a sufficient magnifying power, of the nature of these markings; for they are then clearly seen to be the orifices of tubuli, which pass with great regularity from one surface of the shell to the other, lying nearly parallel to each other, and having their usually straight course interrupted at

Fig. 426.



Portion of transverse section from claw of Crab. Magnified 400 diameters.

tolerably regular intervals by minute sinuositys resembling the "secondary curvatures" described by Prof. Owen in the dentinal tubuli. These sinuositys correspond with bands which are seen to traverse the section, running parallel to the surfaces of the shell; and they appear, like those of dentine, to indicate the successive stages of calcification of the animal basis. This structure is particularly well seen in the black extremities of the claws of the common crab, in which the intertubular substance is quite transparent in a thin section, and of which the hardness and density are as great as in many varieties of dentine; and as the tubuli are seen, in a transverse section of the claw, to radiate from the central cavity towards the surface, the resemblance to a section of a tooth is altogether so close, as quite to deceive an observer unacquainted with the substance he is examining. The same structure exists, however, in the remainder of the shell; but from some difference in its molecular constitution, the intertubular substance has a less dense and tenacious character, and has an opaque chalky aspect, which renders even a very thin

section of it impermeable to light, unless it be saturated with Canada balsam, which then very commonly enters the tubuli, and prevents them from being readily distinguishable. The purpose of the extraordinary density possessed by the extremities of the claws, is evidently to adapt them to the various mechanical uses to which the animal applies them: and it is interesting to see that this is attained without any variation in the organic structure of the part, but merely by a more intimate union, as it would seem, of the solidifying mineral matter with the organic basis. It does not seem improbable that the phosphate of lime, which is known to be present with the carbonate in the shells of Crustacea, may exist in larger proportion towards the extremities of the claws than in other parts of the shell; a question well worthy of chemical investigation.

The periodical *exuviation* of the shell does not appear to be common to all Crustacea; for, according to Mr. Couch*, it does not take place in many of the sessile-eyed tribes, whose cases are as dense as those of the pedunculate orders. It is much to be desired that careful observations should be made on the formation of the new shell in the Crab; since these would probably throw light on much that still remains obscure in the development of dentine.

[The author of the forgoing article is desirous that it should be understood that all the statements contained in it, except such as are expressly made on the authority of others, are the result of his own observations; the general facts regarding the organic structure of the shells of Mollusca, Echinodermata, and Crustacea, having been determined by him in the year 1842, and embodied in a paper read before the Royal Society, Dec. 22 of that year, of which the first of the memoirs cited is an abridgment; and the subject having been subsequently worked out by him in detail, with the aid and encouragement of the British Association, to the reports of which he would refer the reader who may desire additional information as to the results of his researches.]

BIBLIOGRAPHY.—*Carpenter*, On the Microscopic Structure of Shells, in Annals of Natural History, Dec. 1843; and in Reports of British Association for 1844 and 1847. *Bowerbank*, On the Structure of the Shells of Molluscous and Conchiferous Animals, in Transact. of Microscopical Society, vol. i. London, 1844. *G. Valentin*, Anatomie du Genre *Echinus*, in Monographies d'Echinodermes vivans et fossiles, par L. Agassiz: Neufchatel, 1842. *Lavalle*, Recherches d'Anatomie Microscopique sur le test des Crustacés Décapodes; in Annales des Sciences Naturelles, Juin, 1847.